INFLUENCE OF HOSTS ON THE BEHAVIOR OF THE COMMENSAL CRAB PINNOTHERES MACULATUS SAY [1]

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Analysis of factors binding the complex host-commensal relationship is a prelude for an understanding of the community integration and interspecific interactions of marine animals. Extensive accounts of host-commensal partnership have been given by Caullery (1952), Davenport (1955) and Dales (1957). Davenport and his collaborators (1950, 1951, 1953a, 1953b, 1957, 1958 and 1960) showed that a variety of commensals were attracted to their hosts by some diffusible substance released by the host animals. Lucas (1947) pointed out that external metabolites, "ectocrines," play a significant role in establishing the commensal symbiotic relationships.

The commensal crabs, *Pinnotheres maculatus* Say, are present in bay scallops, *Aequipecten irradians concentricus* Say, and penshells, *Atrina rigida* Solander, in Alligator Harbor, Franklin County, Florida. Johnson (1952) demonstrated chemotaxis in pinnotherid crabs with the *Dissodactylus-Mellita* partnership. In view of the frequent occurrence of the crabs in bay scallops and penshells it was decided to examine the host-commensal partnership and to determine to what extent the host affect the crabs.

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Materials and Methods

Bay scallops and penshells were collected in Alligator Harbor, Franklin County, Florida, near the marine laboratory of the Oceanographic Institute, Florida State University. The host animals were maintained in the Oceanographic Institute laboratory in running sea water tables and examined for the presence of crabs immediately after being brought in. The crabs were removed from the hosts and kept in separate running sea water aquaria. In isolation, the crabs were as healthy and active after a period of time as those just removed from the hosts.

To study the attraction of crabs to the hosts, a circular choice apparatus was constructed with plastic material. The principle of circular choice apparatus is well described, with figures indicating the direction of water currents, by Bartel and Davenport (1956). The only difference in the circular choice apparatus used in the present study is that it is larger in size to suit the experimental animals under investigation.

Water circulation in the apparatus was maintained at a steady rate, determined by preliminary flow tests to eliminate the influence of turbulence on the behavior of

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TABLE I

Infestation of bay scallops by Pinnotheres maculatus *in different months of a year*

Month	Scallops examined	No. scallops infested with		% total infestation
		Males	Females	
October, 1957	32	1	7	25.0
June, 1958	15	1	2	20.0
July	142	16	51	47.1
August	98	11	29	40.8
September	7	0	2	28.6
October	18	4	3	38.8
November	13	1	2	23.1

crabs. The water in the apparatus was allowed to circulate for some time before the experimental animals were introduced. A host was introduced first into one of the radial chambers and the system was allowed to come to equilibrium. Then the crabs were introduced into the central chamber. (Hosts were introduced before the crabs because it was found that if both host and commensals were placed at the same time, the crabs began random choice before the responsible factor from the host had sufficient time to become equilibrated in the water circulation of the choice apparatus.) The experiments were conducted in subdued light since the crabs were found to be negatively phototactic; under brightly lighted conditions they remained motionless at the margins of the central chamber.

It was found that 12 hours was sufficient for crabs to make their choice and the number of crabs in each radial chamber was counted after this period. Before and after each experiment the apparatus was thoroughly cleaned with sea water. The behavior of the crabs while seeking hosts was noted. The temperature ranged between 28 and 31° C. during the experimental period. The results were analysed by χ^2 formula (Nass, 1959) to test the significance of distribution among the radial chambers.

TABLE II

Comparison of the average sizes of scallops infested and not infested with crabs

Date of collection	Infested		Not infested		Difference in size between infested and uninfested scallops, mm.
	No. scallops	Average size, mm.	No. scallops	Average size, mm.	
6/27/58	3	37.4	12	40.1	+2.7
7/7/58	5	44.9	18	42.9	−2.0
7/23/58	27	43.9	38	47.5	+3.6
7/30/58	26	49.8	20	52.0	+2.2
8/5/58	17	50.2	15	51.3	+1.1
8/13/58	5	56.2	20	54.7	−1.5
8/23/58	13	54.8	28	57.1	+2.3
9/14/58	2	62.3	5	58.3	−4.0
10/5/58	7	57.9	12	61.8	+3.9
11/14/58	3	66.1	9	64.2	−1.9

Observations

The commensal crabs live between the gill folds in the mantle chamber of scallops and penshells. Rathbun (1917) described the females of this species as commensals, whereas the young stages of males are free-living. The occurrence of male and female crabs in 1957–1958 collections of scallops is shown in Table I. Crabs of both sexes were most abundant during the summer months, and gravid females were found in the same period.

The feeding behavior of the crabs was similar in general to that described for other species of Pinnotheridae (Coupin, 1894; Orton, 1921; Stauber, 1954). Stauber (1945) observed that *Pinnotheres ostreum* caused gill erosions and thickening of the oyster host gills. Parts of the gills of scallops were broken off by the movements of the crabs within the mantle chamber. The average sizes of scallops infested and not infested with crabs are shown in Table II.

Experimental Results

1. *Distribution of crabs in choice apparatus in the absence of hosts*

The crabs were placed in the central chamber of the choice apparatus without hosts in the radial chambers and the distribution at the end of the experimental period was noted. The crabs were sluggish and a few remained in the central chamber at the end of the experiments without making any choice. The χ^2 analysis of results (Table III) indicated that the crabs showed no preference for any of the chambers.

Table III

Distribution of commensal crabs, Pinnotheres maculatus, *in the radial chambers of the choice apparatus in the absence of host influence*

Expt. no.	Crabs		Distribution in radial chambers						χ^2	Critical χ^2 value for 5%
	Tested	Made choice	1	2	3	4	5	6		
1	13	9	4	0	1	1	0	3	9.37	11.98
2	15	13	0	2	2	2	1	6	9.83	11.67
3	14	10	1	5	1	0	1	2	9.55	11.98
4	16	16	3	2	5	2	1	3	3.33	11.52

2. *Attraction of crabs to host scallops*

When a scallop was present in one of the radial chambers, the crabs were very active and moved freely in the central chamber. At the end of the experiments, the crabs were not homogeneously distributed in the radial chambers (Table IV). The crabs showed a statistically significant ($P > .05$) preference for the chamber containing the host, although in one of the seven tests the distribution was random.

The crabs required considerably less time to make their choice than they did in the control experiments. They gathered around the host chamber one after another or in groups. Crabs moving towards the non-host chambers sometimes

Table IV

Attraction of commensal crabs to bay scallops

Expt. no.	Crabs		Distribution in radial chambers						Host vs. non-host	
	Tested	Made choice	1	2	3	4	5	6	χ^2	Critical χ^2 value for 5%
1	8	8	(5)	1	0	0	1	1	11.25	3.57
2	12	12	0	(9)	3	0	0	0	26.98	3.64
3	9	9	1	(7)	1	0	0	0	22.05	3.57
4	11	11	2	0	(3)	0	3	3	0.82	3.64
5	10	10	0	1	0	0	0	(9)	41.61	3.61
6	20	19	2	1	0	(11)	3	2	21.52	3.57
7	16	16	1	1	2	1	(8)	3	12.29	3.68

Parentheses indicate chamber containing bay scallop.

reversed their direction of movement and moved directly into the host chamber. When the crabs moved to an opening leading to a non-host chamber, they remained at the opening for a long time before they made their choice, sometimes moving away from the openings. After entering the host chamber, the crabs gathered around and under the scallops. Some climbed on the upper valve of the scallop and made attempts to enter the host mantle chamber. While some of the crabs gained immediate entry into the host, others were caught between the valves of the host when it contracted, gaining entry when the scallops later opened their valves.

3. *Response when the host water is siphoned into one of the radial chambers*

These experiments were designed to find out if the crabs would respond to water coming from an aquarium containing a host scallop. Water from an aquarium containing a host was siphoned into one of the radial chambers of the choice apparatus. The distance of the host from the crabs in the central chamber was approximately six times greater than in the previous experiments in which the host was placed in a radial chamber. The rest of the procedure was the same as described in the general methods.

Results shown in Table V indicate that the attraction is reduced as compared to

Table V

Choice of crabs when the host water is siphoned into one of the radial chambers

Expt. no.	Crabs		Distribution in radial chambers						Chamber with host water vs. non-host	
	Tested	Made choice	1	2	3	4	5	6	χ^2	Critical χ^2 value for 5%
1	16	14	3	2	(5)	1	1	2	3.47	3.64
2	14	14	(4)	2	2	1	4	1	1.36	3.64

Parentheses indicate chamber into which host water is siphoned.

TABLE VI

Response of crabs to scallop shells with attached animals

Expt. no.	Crabs		Distribution in radial chambers						Chamber with host shell vs. those without host shell	
	Tested	Made choice	1	2	3	4	5	6	χ^2	Critical χ^2 value for 5%
1	14	14	(5)	2	2	3	1	1	3.50	3.68
2	15	12	5	2	0	1	(4)	0	2.28	3.64
3	12	10	0	1	(7)	2	0	0	19.24	3.61
4	15	10	3	0	3	(3)	0	1	0.12	3.61

Parentheses indicate chamber containing the scallop shell.

that of the chambers containing live hosts. The Chi square test showed that crabs were distributed homogeneously in all six radial chambers; the distribution of crabs in the chambers was random.

4. Response of crabs to host shell with attached animals

A variety of sessile animals attach to the outside of the shell of scallops. Scallop shells with attached animals were washed with sea water after the soft parts of the scallops were removed and were tested to find whether the crabs would be attracted to them. The results (Table VI) show that there is no significant attraction of crabs to the shell with attached organisms, except in one of the experiments there is a significant attraction of crabs. This could have resulted from insufficient washing of the shell after removing the soft parts.

5. Response of male commensal crabs to host scallops

Adult males are commensals in their relation with the host, whereas the early male stages are free-living. Experiments were planned to investigate whether the males, removed from the host scallops, respond to the host in the same manner as the females. The results are summarized in Table VII. The males were very active in the presence of the host and occasionally swam within the central chamber of the choice apparatus.

TABLE VII

Response of male commensal crabs to bay scallops

Expt. no.	Crabs		Distribution in radial chambers						Host vs. non-host chambers	
	Tested	Made choice	1	2	3	4	5	6	χ^2	Critical χ^2 value for 5%
1	21	21	3	0	0	0	2	(16)	52.18	3.72
2	17	14	3	(8)	0	2	0	1	15.55	3.64
3	13	13	1	1	2	(9)	0	0	24.41	3.64
4	13	13	2	2	0	1	(8)	0	17.89	3.64

Parentheses indicate chamber with host.

TABLE VIII

Attraction to penshells of crabs removed from bay scallops

Expt. no.	Crabs		Distribution in radial chambers						Host chamber vs. non-host chambers	
	Tested	Made choice	1	2	3	4	5	6	χ^2	Critical χ^2 value for 5%
1	16	16	0	6	(10)	0	0	0	23.23	3.68
2	15	15	0	3	0	0	(11)	1	33.29	3.68
3	16	16	1	0	(11)	1	1	2	30.87	3.68

Parentheses indicate chamber containing penshell.

Chi square analysis of the results indicates that the males were attracted to the scallops. Since no female crabs were present, the attraction of the male crabs appears to be entirely to the host.

6. *Attraction to penshells of crabs removed from scallops*

These experiments were performed to determine whether crabs originally removed from scallops would be attracted to a second host, *Atrina rigida*. Crabs living in the scallops and the penshells are morphologically similar. Penshells of approximately the same weight as scallops used in the earlier experiments were placed in the radial chamber of the choice apparatus and the distribution of the crabs at the end of the experiments was noted. The results (Table VIII) indicate that the crabs were strongly attracted to the penshells.

7. *Preference of crabs between the two hosts, scallops and penshells*

The two hosts, penshells and scallops, were placed in two non-adjacent radial chambers of the choice apparatus and the crabs were introduced in the central chamber. Crabs obtained from scallops showed no statistically significant preference for penshells than for the scallops (Table IX).

TABLE IX

Response of crabs, removed from bay scallops, to penshells and bay scallops when both are present in two separate chambers of the choice apparatus

Expt. no.	Crabs		Distribution in radial chambers						Hosts vs. non-host chambers		Penshells vs. bay scallops	
	Tested	Made choice	1	2	3	4	5	6	χ^2	Critical χ^2 value for 5%	χ^2	Critical χ^2 value for 5%
1	15	15	1	1	(8)	0	3*	2	14.49	5.81	2.50	3.42
2	15	15	(6)	2	1	5*	1	0	10.58	5.81	0.09	3.42

Parentheses indicate chamber with penshell; * indicates chamber with bay scallop.

Discussion

The attraction of commensals to their hosts in response to some diffusible substance or substances released from hosts was demonstrated by Welsh (1930), Thorpe and Jones (1937) and Davenport (1950, 1953a). The present experiments showed that the commensal crab, *Pinnotheres maculatus,* is capable of recognizing its hosts, *Aequipecten irradians* and *Atrina rigida,* under the described experimental conditions. The active movements of the commensal crabs in the presence of the hosts seem to be stimulated by some attractant from the host. The attraction of commensals to the host scallops decreased when the hosts were not directly introduced in the radial chamber of the choice apparatus. This suggests that perhaps a spatial proximity of hosts to commensals is necessary for demonstration of attraction under experimental conditions. The decreased attraction could have resulted either from a gradient or a highly diffusible nature of the attractant.

The absence of attraction of commensals to empty host shells, with attached epizooites, indicates that the source of the attractant is the soft parts of the scallops.

The experiments with males of *P. maculatus* demonstrated conclusively that their response to scallops is equal to that of the females of the same species. It is not known from the present study how the free-living early stages of males change to commensal habit in their adult stage. Experiments with free-living early-stage males might reveal the nature of this change.

Crabs removed from scallops were attracted readily to *Atrina rigida,* another host which inhabits the same general locality as the scallops. The results of experiments indicate that both scallops and penshells release attractants that stimulate the crab to seek the hosts. The attraction of crabs from scallops to both the hosts appears to be equal when both are simultaneously tested for response. Crabs living in the scallops and those in the penshells are morphologically similar, and crabs from scallops are not physiologically host-specific. Reciprocal experiments with crabs obtained from penshells should elucidate the specificity of these commensal crabs.

Summary

1. Experiments using a circular choice apparatus showed a statistically significant attraction of commensal crabs, *Pinnotheres maculatus*, to bay scallops, *Aequipecten irradians concentricus,* and penshells, *Atrina rigida.*

2. The adult males of *P. maculatus* removed from bay scallops showed a significant attraction to the host.

3. When tested for preference between the two hosts, crabs removed from bay scallops showed no preference for one host over the other. The attraction of crabs to both the hosts was statistically significant. Experiments suggested that the crabs removed from scallops are not host-specific.

LITERATURE CITED

Bartel, A. H., and D. Davenport, 1956. A technique for the investigation of chemical responses in aquatic animals. *Brit. J. Anim. Behav.,* **4**: 117–119.

Caullery, M., 1952. Parasitism and Symbiosis. Sidgwick and Jackson, London.

Coupin, H., 1894. Sur l'alimentation de deux commensaux (*Nereilepas* et *Pinnotheres*). *C. R. Acad. Sci. Paris,* **119**: 540–543.

Dales, R. P., 1957. Interrelation of organisms. A Commensalism. Treatise on marine ecology and paleoecology. *Geol. Soc. America., Memoir, 67,* **1**: 391–412.

DAVENPORT, D., 1950. Studies in the physiology of commensalism. I. The polynoid genus *Arctonoë*. *Biol. Bull.*, **98**: 81–93.

DAVENPORT, D., 1953a. Studies in the physiology of commensalism. III. The polynoid genera *Acholoe, Gattyana* and *Lepidasthenia*. *J. Mar. Biol. Assoc.*, 32: 161–173.

DAVENPORT, D., 1953b. Studies in the physiology of commensalism. IV. The polynoid genera *Polynoe, Lepidasthenia* and *Harmothoe*. *J. Mar. Biol. Assoc.*, 32: 273–288.

DAVENPORT, D., 1955. Specificity and behavior in symbiosis. *Quart. Rev. Biol.*, **30**: 29–46.

DAVENPORT, D., AND J. F. HICKOK, 1951. Studies in the physiology of commensalism. II. The polynoid genera *Arctonoë* and *Halosydna*. *Biol. Bull.*, **100**: 71–83.

DAVENPORT, D., AND K. S. NORRIS, 1958. Observations on the symbiosis of the sea anemone *Stoichactis* and the pomocentrid fish, *Amphiprion percula*. *Biol. Bull.*, **115**: 397–410.

DAVENPORT, D., G. CAMOGUIS AND J. F. HICKOK, 1960. Analysis of the behavior of commensals in host factor. I. A. Hesionid polychaete and a pinnotherid crab. *Brit. J. Anim. Behav.*, **8**: 209–218.

HICKOK, JOHN F., AND D. DAVENPORT, 1957. Further studies in the behavior of commensal polychaetes. *Biol. Bull.*, **113**: 397–406.

JOHNSON, I. S., 1952. The demonstration of host factor in commensal crab. *Trans. Kansas. Acad. Sci.*, **55**: 485–464.

LUCAS, C. E., 1947. The ecological effects of external metabolites. *Biol. Rev.*, **22**: 270–295.

NASS, C. E., 1959. The χ^2 test formula for small expectations in contingency tables, with special reference to accidents and absenteeism. *Biometrica,* **46**: 365–385.

ORTON, J. H., 1921. The mode of feeding and sex phenomenon in the pea crab (*Pinnotheres pisum*). *Nature,* **106**: 533–534.

RATHBUN, M. J., 1917. The grapsoid crabs of America. *Bull. U. S. Nat. Mus.*, No. 97, 461 pp. 161 pl.

STAUBER, L. A., 1945. *Pinnotheres ostreum,* parasitic on the American oyster, *Ostrea* (*Gryphea*) *virginica*. *Biol. Bull.*, **88**: 269–291.

THORPE, W. H., AND F. G. W. JONES, 1937. Olfactory conditioning in parasitic insects and its relation to host selection. *Proc. Roy. Soc. London, Ser. B,* **124**: 56–81.

WELSH, J. H., 1930. Reversal of phototropism in a parasitic water mite. *Biol. Bull.*, **59**: 165–169.